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Variance component analysis of plant architectural traits and fruit yield in melon

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Summary A cross was made between a unique highly branched, early flowering line, U. S. Department of Agriculture (USDA) 846-1 (P_1; 7 to 11 lateral branches), and 'Topmark' (P_2; 2 to 4 lateral branches), a U.S. Western Shipping melon, to produce an array of 119 F_3 families. Subsequently, a genetic analysis was conducted at Arlington and Hancock, Wisconsin in 2001 to evaluate the segregating progeny for factors likely involved in yield-formation, including days to anthesis, percentage of plants with early pistillate flowering, primary branch number, fruit number and weight per plant, average weight per fruit, percentage of plants with predominantly crown fruit set, and percentage of plants with early maturing fruit. Although, genotype × environment (G × E) interactions were important for some traits (e.g., fruit number and fruit weight), considerable additive and/or dominance variance was detected for all traits. This research provides critical data associated with highly branched melon germplasm including trait correlations and heritabilies (broad- and narrow-sense ranged between 0.28 and 0.91) that used judiciously will allow the development high yielding melon cultivars with early, basally concentrated fruit suitable for once-over or machine harvesting operations.

Keywords *Cucumis melo* L. · Exotic germplasm · Heritability estimation · Primary branch number · Yield components

Abbreviations

AWF	average weight per fruit
BLUE	best linear unbiased estimation
BLUP	best linear unbiased prediction
DA	days to anthesis
FN	fruit number per plant
FW	fruit weight per plant
PB	primary branch number
PCF	percentage of plants with predominantly crown fruit set
PMF	percentage of plants with early maturing fruit
PPF	percentage of plants with early pistillate flowering

Melon (*Cucumis melo* L.) is an economically important, cross-pollinated, vegetable species. Worldwide, more than 18 million MT of melons were produced in 1999, with China, Turkey, Iran the United States, and

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Spain being the major producers (F.A.O. 1997; F.A.O. 1999). In 2003, over one million MT of Western Shipping and Eastern Market type melons (Group Cantalupensis) were produced in the U.S., having a market value of almost $400 million U.S. (N.A.S.S. 2003).

Cantaloupe yield in the U.S. has increased from 7.5 MT/acre in 1992 to 11.5 MT/acre in 2003 (N.A.S.S. 2003). However, most of this yield improvement can be credited to improved cultural practices, breeding for relatively simple traits such as resistance to diseases and pests, and the use of hybrids created from sparingly few elite lines (McCreight et al. 1993; Robinson and Decker-Walters 1997). Continued yield increases in melon will likely depend on the preservation, availability, and use of genetic variability (e.g., exotic germplasm), and breeding for yield or related traits.

Due to the complex inheritance of yield-related traits and their low heritabilities, breeding for yield in many crop species has been difficult (Board et al. 2003; Septiningsih et al. 2003; Vidal-Martinez et al. 2001; Yadav et al. 1998). In melon, genetic studies of plant architecture and fruit yield (e.g., days to anthesis, plant architecture, and fruit number, weight, and maturity; hereafter denominated yield-formation traits or factors) have been limited (Lippert and Legg 1972; Lippert and Hall 1982). Moreover, estimates of realized heritability (h_r^2) of early yield ($h_r^2 = 0.13$), fruit number per plant ($h_r^2 = 0.12$), fruit weight per plant ($h_r^2 = 0.09$), and average fruit weight ($h_r^2 = 0.52$) have been reported to be relatively low or at most moderately high (Lippert and Hall 1982).

Efficient selection for yield in melon requires the estimation of genetic parameters (e.g., variance components, heritabilities, and gene number) for the strategic planning and allocation of limited resources (i.e., choice of selection method and extent of evaluation over locations and years). North Carolina Designs I, II, III, (Comstock and Robinson 1948, 1952) diallel analysis (Griffing 1956), and/or variance component analysis of advanced generation families (e.g., F_3; Mather and Jinks 1982) have proven efficient for the estimation of the genetic parameters and environmental variance associated with quantitative traits (Cockerham 1954; Hallauer and Miranda 1988; Lande 1981).

Initial variance component analyses using F_3 families is of particular tactical value in melon breeding when weighing the cost of advanced populations and inbred progenies development [e.g., space and relatively low (20%) pollination success] during plant improvement. Therefore, a genetic analysis of F_3 families was performed to provide estimates of variance component estimates (i.e., genetic, environmental, and G × E), broad- and narrow-sense heritabilities, and least number of effective factors of yield-formation traits in a unique highly branched melon population. This study provides an understanding of the genetics of yield-formation traits in a melon population derived from exotic germplasm that has potential for yield improvement.

Materials and methods

Plant materials

Horticulturally unique germplasm designated CR (received in 1995 from Mr. Claude Hope, Cartago, Costa Rica) was obtained from the U.S. Department of Agriculture, Agricultural Research Service (USDA, ARS) melon breeding project, Madison, Wisconsin. This accession, C. *melo* ssp. *agrestis* (Naud.) Pangalo, is characterized by a "fractal" or radiant growth habit (Prusinkiewicz and Haran 1989; Smith 1984). CR is early flowering, monoecious, fast growing, indeterminate, possesses standard size internodes, abundant branching (6 to 12 primary branches), and bears many small fruits (up to 100 fruits/plant) 3–6 cm in diameter (Zalapa 2005; Zalapa et al. 2007). The fractal architecture of CR is distinct from the vining (Rosa 1924), dwarf (Mohr and Knavel 1966), and birdnest (Paris et al. 1981) plant habits, and its unique habit is a function of internode length (standard size) coupled with a comparatively high number of primary, secondary, and tertiary branches.

A monoecious, early flowering CR plant having 12 primary branches was selected in 1996, and was subsequently crossed to an F_1 plant derived from a cross between andromonoecious USDA lines FMR#8 and SC#6. A monoecious, early flowering plant was then selected and self-pollinated four times to produce an S_3 inbred line designated USDA 846-1. This monoecious, fractal, highly branched (5 to 8 primary branches) line produces a concentrated fruit-

set (2–5 fruits near the crown of the plant), and is capable of multiple fruiting cycles (Zalapa 2005; Zalapa et al. 2007).

USDA 846-1 (P_1) was crossed to 'Topmark' (P_2), which is andromonoecious, possesses between two to four lateral branches, and produces a diffuse, distal fruiting setting habit typical of commercial vining melon types. A single F_1 plant from this initial mating was self-pollinated to generate F_2 individuals, which were subsequently used to produce 119 F_3 families.

Experimental design

Seeds from P_1, P_2, F_1, and 119 F_3 families and a control cultivar, 'Hale's Best Jumbo' (HB; Excel Seeds, Chattanooga, Tenn.), were sown in 72-unit plastic potting trays (T. O. Plastics, Inc., Clearwater, MN) containing Growing Mix No. 2 (Conrad Fafard, Inc., Agawam, Mass.). Trays were held in a greenhouse at the University of Wisconsin-Madison (UW) during the spring of 2001, watered once a day, and fertilized (N:P:K = 20:20:20) twice before transplanting. Three-week old seedlings were "hardened-off" for three days, fertilized with starter fertilizer (N:P:K = 10:24:8), and transplanted (from June 4 to 8) to rows covered with 1 mm black plastic at the UW experimental farms at Arlington (AR) and Hancock (HCK), Wisc. Plants were spaced 0.70 m within rows on 2 m centers (7,143 plants/ha), and standard cultivation practices were followed according to UWEX (2001) for Hancock's Planefield loamy sand (Typic Udipsamment) and Arlington's Plano silt loam (Typic Argiudoll) soil. Although this planting density is lower than that used commercially (14,285 plants/ha), it allowed for data collection on individual plants for estimation of genetic parameters. The experimental design was a randomized complete block design (RCBD) consisting of three blocks with 10 plants per plot. 'Hale's Best Jumbo' (HB) was used to provide a benchmark for maturation rate and harvest timing.

Data collection

Days to anthesis (DA) was recorded as the days from transplanting to the time when approximately 50% of the plants in a plot possessed at least one open flower. The percentage of plants with early pistillate flowering (PPF) was calculated on a per plot basis by dividing the number of plants in a plot having at least one fully expanded pistillate flower at/or before 40 days after transplant by the total number of plants per plot and multiplying by 100. The number of primary branches (PB) for each plant was counted 30 days after transplanting to include all branches of more than 12.5 cm in length below the fourth node. Fruit number (FN) and fruit weight (FW; kg) data were collected per plant 80 days after transplanting using all fruit of at least 7.5 cm in diameter. The average weight per fruit (AWF; kg) was calculated for each plant by dividing the total fruit weight per plant by the total fruit number. The percentage of plants with predominantly crown fruit set (PCF) was calculated per plot by dividing the number of plants in a plot having at least 50% of all fruits concentrated near the crown of the plant by the total number plants in that plot and multiplying by 100. The percentage of plants with early maturing fruit (PMF) was calculated per plot by dividing the number of plants in a plot having at least one mature fruit (fruit assessed by their fruit scar, color, aroma, netting, and flesh color) at the time of harvest (80 days after transplant) by the total number of plants in that plot and multiplying by 100. Days to anthesis and early pistillate flowering data were collected only at AR, while data on all other traits were collected at both AR and HCK.

Analysis of variance

The PROC UNIVARIATE procedure of SAS (SAS 1999) was used to generate stem and leaf displays and box and normal probability plots, and the Shapiro–Wilk statistic was employed to test F_3 family distributions for normality. Analyses of variance (ANOVA) was performed using the PROC MIXED COVTEST METHOD TYPE3 procedure of SAS (SAS 1999). Additionally, variance components were estimated employing restricted maximum likelihood (REML), and each variance estimate was tested for significance using the likelihood ratio statistic (Littell et al. 1996). The linear random-effects model for such analyses was the following: $Y = \mu + L + B(L) + F + L \times F + B(L) \times F + e$; where Y is the trait (e.g., number of primary branches), μ is the

common effect, L is the location effect, B(L) is the block within location effect, F is the effect of the F_3 families, L × F is the location × F_3 families interaction effect, B(L) × F is the block within location × F_3 families interaction effect, and e is the plant-to-plant variation within F_3 families. Analyses of F_3 families were also performed by location for all traits. The variation within F_3 families was further partitioned into that due to heterogeneous effects within each F3 family and environmental effects (i.e., variation among heterogeneous entries minus the variation among homogenous entries).

Best linear unbiased predictions (BLUPs), their standard errors, (S.E.), and confidence intervals (95%) (C.I.s) were estimated for each F_3 family examined using the SOLUTION option of the RANDOM statement of the PROC MIXED COVTEST procedure (SAS 1999; Bernardo 1996a, 1996b, 1998). The two parental inbred lines (P_1 and P_2) and their F_1 hybrid (collectively denominated as homogeneous entries) were analyzed independently in order to obtain plant-to-plant variation estimates, which provided a measure of environmental effects (Hallauer and Miranda 1988). Variance components for such homogenous entries were estimated by REML using a linear mixed-effects model, where P_1, P_2, and their F_1 hybrid were considered as fixed effects (Littell et al. 1996). Best linear unbiased estimations (BLUEs) were calculated for P_1, P_2, their F_1 hybrid, and HB using the SOLUTION option of the model statement of the PROC MIXED COVTEST procedure (SAS 1999).

The 95% C.I.s of F_3 progeny BLUPs and the BLUEs of the parental lines, their hybrid, and HB were used for comparisons of performance among genotypes. When the BLUE of the parental lines, their hybrid, and/or HB were outside the C.I. limit of the BLUP of the F_3 progenies, such genotypes were considered to be significantly ($P \leq 0.05$) different from each other (de Leon et al. 2005). To determine heterotic patterns and the percentage of transgressive segregants above or below each parent, the BLUP value of each family was compared to the BLUE value of each parent and the mid-parent estimate [the BLUE of $(P_1 + P_2)/2$].

In order to assess whether G × E interactions were due to trait magnitude changes between locations or changes in the direction of the response (i.e., F_3 family rank changes), Spearman (rank) correlation coefficients (r_s) were calculated using F_3 family data for each individual trait across locations following the same general methodology used by Yan and Rajcan (2003). When the correlation coefficient between data across locations was $r_s \leq 0.5$, G × E interactions were considered more likely to be due to F_3 family rank changes, and when $r_s \geq 0.5$, G × E interactions were considered more likely to be due to trait magnitude changes between locations.

Phenotypic and genotypic correlations

Phenotypic correlations (r; $n = 119$) between pairs of traits were calculated by location using the PROC CORR with the SPEARMAN option (SAS 1999).

Genetic variance estimates

Expected genetic variance components of F_3 families were estimated using the methods of Mather and Jinks (1982) as applied by Hallauer and Miranda (1988). F_3 family data allowed for the estimation of two sources of genetic variation: (1) variation among F_3 progeny means $\left(\sigma^2_{\bar{F}3}\right)$, and; (2) mean variation of F_3 progenies $\left(\bar{\sigma}^2_{\bar{F}3}\right)$. The variation among F_3 progeny means, which has an expectation of $\sigma^2_{\bar{F}3} = \sigma^2_A + 1/4\sigma^2_D$, where σ^2_A and σ^2_D are the additive and dominance genetic variances, respectively, and its standard error (S.E.) were obtained for each trait directly from the PROC MIXED output from the variance among F_3 family means. The mean variation of F_3 progenies, which has an expectation of $\bar{\sigma}^2_{F3} = 1/2\sigma^2_A + 1/2\sigma^2_D$, was calculated by subtracting the variance among plants ($\sigma^2_{P\cdot}$) within homogenous entries (P_1, P_2, and F_1) from the variance among plants within F_3 families ($\sigma^2_{\bar{P}}$). After solving $\sigma^2_{\bar{F}3} = \sigma^2_A + 1/4\,\sigma^2_D$ and $\bar{\sigma}^2_{F3} = 1/2\,\sigma^2_A + \sigma^2_D$, estimates of σ^2_A and σ^2_D were calculated as $\sigma^2_A = [4\,\sigma^2_{\bar{F}3} - 2(\bar{\sigma}^2_{F3})]/3$, and $\sigma^2_D = [8\bar{\sigma}^2_{F3} - 4(\sigma^2_{\bar{F}3})]/3$. Approximate and conservative of standard errors (S.E.) for these genetic estimates were calculated using the following formulas derived from Hallauer and Miranda (1988):

$$\text{S.E.}(\sigma^2_A) = \text{Sqrt}[\text{Var}(\sigma^2_A)] = \text{Sqrt}\{[16\text{Var}(\sigma^2_{F3}) + 4\text{Var}(\sigma^2_P) + 4\text{Var}(\sigma^2_{P'})]/9\},$$

and

$$\text{S.E.}(\sigma^2_D) = \text{Sqrt}[\text{Var}(\sigma^2_D)] = \text{Sqrt}\{[64\text{Var}(\sigma^2_P) + 64\text{Var}(\sigma^2_{P'}) + 16\text{Var}(\sigma^2_{F3})]/9\}$$

Estimation of heritabilities

Both narrow- and broad-sense heritabilities were estimated based on individual plants within F_3 families and F_3 family means. Negative or nearly zero values of σ^2_A or σ^2_D were taken as zero for the estimation of heritability calculations, which were adjusted by removing the appropriate parameter. Heritability standard errors were approximated using the general approach followed by Hallauer and Miranda (1988). The narrow-sense heritabilities of individual plants within F_3 families (h^2_{NP}) were estimated as $h^2_{NP} = 1/2\sigma^2_A/\sigma^2_{PP}$, where σ^2_A and σ^2_{PP} are the additive genetic variance and the phenotypic variance of individual plants within F_3 families, respectively. The phenotypic variance based on individual plants within F_3 families (i.e., $\sigma^2_{PP} = \sigma^2_P$) at each location was obtained directly from the SAS output from the variance among plants within F_3 families. The standard error (S.E.) of the narrow-sense heritabilities of individual plants within F_3 families was calculated as $\text{S.E.}(h^2_{NP}) = 1/2[\text{S.E.}(\sigma^2_A)]/(\sigma^2_{PP})$. The narrow-sense heritabilities based on F_3 family means (h^2_{NF}) were estimated as $h^2_{NF} = 1.0166\sigma^2_A/\sigma^2_{PF}$, where σ^2_A and σ^2_{PF} are the additive genetic variance and the phenotypic variance based on F_3 family means, respectively, and the estimate of σ^2_A was adjusted for family size (i.e., 30) using coefficients proposed by Kearsey and Pooni (1996). The phenotypic variances based on F_3 family means at each location was estimated as $\sigma^2_{PF} = (\sigma^2_{PP} + P\sigma^2_{B\times F} + bp\sigma^2_{F3})/bp$; where b, p, σ^2_{pp}, $\sigma^2_{B\times F}$, and (σ^2_{F3}) refer to the number of block, number of plants per plot, the variance among plants within F_3 families, the variance due to F_3 family × block interaction, and the variance among F_3 family means, respectively. The standard error (S.E.) of the narrow-sense heritabilities based on F_3 family means was calculated as $\text{S.E.}(h^2_{NF}) = 1.0166[\text{S.E.}(\sigma^2_A)]/\sigma^2_{PF}$.

Broad-sense heritabilities of individual plants within F_3 family (h^2_{BP}) were calculated as $h^2_{BP} = (1/2\sigma^2_A + 1/2\sigma^2_D)/\sigma^2_{PP}$, where σ^2_A, σ^2_D, and σ^2_{PP} are the additive genetic variance, dominance genetic variance, and phenotypic variance of individual plants within F_3 families, respectively. The standard error of broad-sense heritabilities of individual plants within F_3 families were calculated as $\text{S.E.}(h^2_{BP}) = \{1/2[\text{S.E.}(\sigma^2_A)] + 1/2[\text{S.E}(\sigma^2_D)]\}/(\sigma^2_{PP})$. The broad-sense heritabilities based on F_3 family means (h^2_{BF}) were calculated as $h^2_{BF} = (1.0166\sigma^2_A + 0.266\sigma^2_D)/\sigma^2_{PF}$, where σ^2_A, σ^2_D, and σ^2_{PF} are the additive genetic variance, dominance genetic variance, and phenotypic variance based on F_3 family means, respectively, and the estimates σ^2_A and σ^2_D were adjusted for family size (i.e., 30) using the coefficients proposed by Kearsey and Pooni (1996). The standard error of broad-sense heritabilities based on F_3 family means were calculated as $\text{S.E.}(h^2_{BF}) = \{1.0166[\text{S.E.}(\text{S.E.}\sigma^2_A)] + 0.266[\text{S.E.}(\sigma^2_D)]\}/\sigma^2_{PF}$.

Estimation of the minimum number of effective factors

The minimum number of effective factors (n) influencing yield yield-formation traits was estimated according to Castle (1921) and Wright (1968) using the correction factor suggested by Cockerham (1986) as $n = [(\bar{P}_1 - \bar{P}_2)^2 - (\sigma^2_{\bar{P}_1} + \sigma^2_{\bar{P}_2})]/(8 \times \sigma^2_A)$, where $\bar{P}_1$ and $\bar{P}_2$ are the estimates of the mean yield of parents P_1 and P_2; $\sigma^2_{\bar{P}_1}$ and $\sigma^2_{\bar{P}_2}$, are the estimates of variance of two parental lines means, and σ^2_A is the additive genetic variance.

Results

Statistical evaluation of locations, genotypes (i.e., F_3 families), and genotype x location interaction effects using combined (AR and HCK) trait data are presented in Tables 1 and 2. Analyses of variance revealed significant differences ($P \leq 0.01$ or $P \leq 0.05$) in all sources of variation (i.e., locations, genotype, and genotype x location interactions), except for locations for primary branch number and percentage of early maturing fruit. Likelihood ratio tests of the variance component analyses indicated that locations were not a significant ($P \geq 0.05$) source of variation for any trait

Table 1 Analysis of variance, estimates of variance components, and Spearman correlation (rank) coefficients (r_s) between locations for primary branch number and fruit number and weight (kg) per plant in 119 F_3 melon (*Cucumis melo* L.) families derived from a cross between USDA 846-1 (P_1) and 'Topmark' (P_2) grown at Arlington and Hancock, Wisconsin in 2001

Source of variation	Primary branch number		Fruit number per plant		Fruit weight per plant (kg)	
	df[a]	MS[b]	df	MS	df	MS
Location [L]	1	47.33 n.s.[c]	1	14,767**	1	11,243**
Block (Location) [B(L)]	4	15.84**	4	31.07**	4	173.39**
Family [F]	118	2.83**	118	26.17**	118	13.53**
Family × Location [F × L]	118	13.06*	118	11.61**	118	6.81**
Family × Block (Location) [F × B(L)]	472	2.39**	472	5.19**	472	3.44**
Plants within families [P]	6,210	0.79	6,059	2.23	5,788	1.42
Total	6,923		6,772		6,501	
	Variance component	Percent of total[d]	Variance component	Percent of total	Variance component	Percent of total
Location [L]	0.01 ± 0.02 n.s.	0.8	4.44 ± 6.29 n.s.	59.2	3.57 ± 5.12 n.s.	63.5
Block (Location) [B(L)]	0.01 ± 0.01 n.s.	1.0	0.02 ± 0.02 n.s.	0.3	0.15 ± 0.11 n.s.	2.6
Family [F]	0.17 ± 0.03**	14.8	0.27 ± 0.07**	3.6	0.13 ± 0.04**	2.4
Family × Location [F × L]	0.02 ± 0.01*	2.0	0.23 ± 0.05**	3.0	0.13 ± 0.03**	2.3
Family × Block (Location) [F × B(L)]	0.16 ± 0.02**	14.0	0.31 ± 0.04**	4.1	0.22 ± 0.02**	3.9
Plants within families [P]	0.79 ± 0.01**	67.4	2.23 ± 0.04**	29.7	1.42 ± 0.03**	25.2
Total	1.17	100	7.49	100	5.62	100
(r_s)	0.72**		0.53**		0.47**	

[a] df = degrees of freedom

[b] MS = mean squares

[c] *, **, n.s. indicates that the effect is significant at $P \leq 0.05$, $P \leq 0.01$, and not significant, respectively

[d] Percent of variance component contribution to the total variance

examined. However, the location effect was a greater source of variation (i.e., higher percentage contribution to the total variance) than the genotype and genotype x location interaction main effects for all traits, except for primary branch number and early maturing fruit. Likelihood ratio tests of the variance component analyses revealed significant variation ($P \leq 0.05$) for genotype and genotype x location interaction effects for all traits examined. The percentage of variation contributed by F_3 families ranged from 2.4 % (fruit weight) to 18.8 % (early maturing fruit), and the variation percentage contributed by genotype x location interaction main effects ranged from 0.9 % (average weight per fruit) to 18.5 % (early maturing fruit).

Comparisons of Spearman (rank) correlations coefficients (r_s) of F_3 families for each trait across locations (i.e., AR vs.HCK) indicated that while all correlations were highly significant ($P \leq 0.01$), the lowest correlation coefficient between locations was obtained for early maturing fruit ($r_s = 0.32$) and the highest was for primary branch number ($r_s = 0.72$) (Table 1). Given the significant location and/or genotype x location interactions detected for all traits, subsequent analyses are presented by location.

Parent and F_3 families BLUPs

The Shapiro-Wilk tests for normality indicated that the phenotypic distributions of the F_3 families for all traits were normally distributed (data not presented; Zalapa 2005). The BLUEs of USDA 846-1 (P_1), 'Topmark' (P_2), their hybrid (F1), and 'Hale's Best Jumbo' (HB) along with the F_3 population (individual F_3 families data not presented; Zalapa 2005) BLUPs and their C.I.s for each trait examined are presented in Table 3. The performance of P_1 was consistently higher that of P_2, F_1, and HB for days to anthesis,

Table 2 Analysis of variance, estimates of variance components, and Spearman correlation (rank) coefficients (r_s) between locations for average weight per fruit (kg), percentage of plants possessing predominantly crown fruit set per plot, and percentage of plants with early maturing fruit per plot in 119 F_3 melon (*Cucumis melo* L.) families derived from a cross between USDA 846-1 (P_1) and 'Topmark' (P_2) grown at Arlington and Hancock, Wisconsin in 2001

Source of variation	Average weight per fruit (kg)		Percentage of plants with predominantly crown fruit set/plot		Percentage of plants with early maturing fruit/plot	
	df[a]	MS[b]	df	MS	df	MS
Location [L]	1	185.33**[c]	1	80,829*	1	25222 n.s.
Block (Location) [B(L)]	4	2.89**	3	5,182.91**	3	10200**
Family [F]	118	3.32**	118	1,040.08**	118	1347.87**
Family × Location [F × L]	118	0.48*	118	488.59**	118	672.15**
Family × Block (Location) [F × B(L)]	472	0.39**	354	351.14	354	353.23
Plants within families [P]	5788	0.24	–[d]	–	–	–
Total	6501		594		594	
	Variance component	Percent of total[e]	Variance component	Percent of total	Variance component	Percent of total
Location [L]	0.062 ± 0.089 n.s.	16.6	264.2 ± 400.51 n.s.	31.0	51.4 ± 128.25 n.s.	6.7
Block (Location) [B(L)]	0.002 ± 0.002 n.s.	0.6	40.68 ± 35.56 n.s.	4.8	82.78 ± 69.99 n.s.	10.7
Family [F]	0.054 ± 0.008**	14.4	125.17 ± 34.98**	14.7	144.98 ± 42.44**	18.8
Family × Location [F × L]	0.003 ± 0.002*	0.9	79.38 ± 30.13**	9.3	142.64 ± 38.7**	18.5
Family × Block (Location) [F × B(L)]	0.016 ± 0.003**	4.3	341.79 ± 25.02**	40.2	349.85 ± 26.01**	45.3
Plants within families [P]	0.237 ± 0.004**	63.3	–	–	–	–
Total	0.374	100	851.22	100	771.64	100
(r_s)	0.61**		0.42**		0.32**	

[a] df = degrees of freedom

[b] MS = mean squares

[c] *, **, n.s. indicates that the effect is significant at $P \leq 0.05$, $P \leq 0.01$, and not significant, respectively

[d] Calculations not available due to model partitioning

[e] Percent of variance component contribution to the total variance

early pistillate flowering, primary branch number, predominantly crown fruit set, and early maturing fruit, and was significantly higher ($P \leq 0.05$) than the performance of the F_3 population taken collectively for each of these traits. Performance, changes in genotype (i.e., P_1, P_2, F_1, HB, and F_3 families) across locations were observed for fruit number and weight, and average weight per fruit. Heterotic values in the F_1 generation were detected for days to anthesis, early pistillate flowering, fruit number and weight, average weight per fruit, predominantly crown fruit set, and early maturing fruit. Individual F_3 families transgressed the performance of at least one parent for all traits examined, except for primary branch number (Table 4).

Phenotypic correlations

Phenotypic correlations among traits are presented in Table 5. Days to anthesis (DA) was negatively correlated with early pistillate flowering (PPF) ($r = -0.58$; AR) and early maturing fruit (PMF) ($r = -0.24$; AR). The percentage of plants with early pistillate flowering was negatively correlated with fruit number (FN) ($r = -0.21$; AR), and positively correlated with average weight per fruit (AWF)

Table 3 Best linear unbiased estimations (BLUEs), best linear unbiased predictions (BLUPs), standard errors (S.E.), and confidence intervals (C.I.) for melon (*Cucumis melo* L.) yield-formation factors of USDA 846-1 (P_1), 'Topmark'(P_2), their hybrid (F_1) and F_3 progeny ($P_1 \times P_2$), and 'Hale's Best Jumbo' (HB) based on plants grown at Arlington and Hancock, Wisconsin in 2001

Arlington	BLUE				BLUP	C.I. (95%)	
Trait	P_1	P_2	F_1	HB	F_3 families	Lower	Upper
Days to anthesis	33.50**[a]	35.40**	33.90**	34.20 n.s.[b]	34.62 ± 0.15	33.97	35.28
Percentage of plants with early pistillate flowering/plot	46.67**	16.67 n.s.	50.00**	60.00**	29.54 ± 3.55	14.26	44.82
Primary branch number	6.70**	4.10**	5.60 n.s.	3.90**	5.33 ± 0.10	4.90	5.77
Fruit number/plant	3.60**	5.10 n.s.	5.63**	4.40 n.s.	4.70 ± 0.14	4.08	5.32
Fruit weight/plant (kg)	4.05 n.s.	4.97 n.s.	6.03 n.s.	5.89 n.s.	5.09 ± 0.31	3.75	6.43
Average weight/fruit (kg)	1.15 n.s.	1.03**	1.10 n.s.	1.40 n.s.	1.24 ± 0.04	1.06	1.41
Percentage of plants predominantly crown fruit set/plot	70.00**	5.00**	10.00 n.s.	5.00**	14.09 ± 2.39	5.26	22.92
Percentage of plants with early maturing fruit/plot	66.67**	1.67**	66.67**	41.67**	22.45 ± 10.88	7.31	37.60
Hancock							
Primary branch number	7.10**	4.30**	5.70 n.s.	4.60**	5.50 ± 0.05	5.28	5.72
Fruit number/plant	2.20**	1.50 n.s.	1.44 n.s.	1.60 n.s.	1.72 ± 0.07	1.41	2.03
Fruit weight/plant (kg)	2.74**	2.20 n.s.	2.27 n.s.	2.65**	2.40 ± 0.06	2.14	2.65
Average weight/fruit (kg)	1.49 n.s.	1.61 n.s.	1.72**	1.85**	1.59 ± 0.03	1.47	1.71
Percentage of plants predominantly crown fruit set/plot	56.67**	10.00**	43.33 n.s.	43.33 n.s.	37.63 ± 4.83	16.85	58.40
Percentage of plants with early maturing fruit/plot	56.67**	30.00 n.s.	50.00**	53.33**	35.47 ± 2.95	22.80	48.15

[a] **The BLUE of a parental line (i.e., P_1 and P_2), their hybrid, and/or 'Hale's Best Jumbo' considered significantly different ($P \leq 0.05$) from the average of the F_3 families when values were outside the C.I. limit of the F_3 progeny population BLUP

[b] n.s., the BLUE of the a parental line, their hybrid, and/or 'Hale's Best Jumbo' considered not significantly different ($P \geq 0.05$) from the average of the F_3 families when values were within the C.I. limit of the F_3 progeny population BLUP

($r = 0.24$; AR) and PMF ($r = 0.24$; AR). Primary branch was positively correlated with predominantly crown setting fruit (PCF) ($r = 0.25$; AR), FN ($r = 0.23$; HCK), and fruit weight (FW) ($r = 0.20$; HCK), and negatively correlated with AWF ($r = -0.21$; HCK). Fruit number was positively correlated with FW ($r = 0.47$ and $r = 0.61$, AR and HCK, respectively), and negatively correlated with AWF ($r = -0.76$ and $r = -0.70$, AR and HCK, respectively), PCF ($r = -0.52$ and $r = -0.48$, AR and HCK, respectively), and PMF ($r = -0.28$; HCK). Fruit weight was positively correlated with AWF ($r = 0.27$; HCK), and negatively correlated with PCF ($r = -0.3$ and $r = -0.22$, AR and HCK, respectively) and PMF ($r = -0.21$ and $r = -0.20$, AR and HCK, respectively). Average weight per fruit was positively correlated with PCF ($r = 0.41$ and $r = 0.32$, AR and HCK, respectively), and PCF was positively correlated with PMF ($r = 0.36$ and $r = 0.8$, AR and HCK, respectively).

Genetic variance estimates

Negative estimates of variance components (Table 6) were assumed to be zero (Robinson et al. 1955), and are reported herein as a historical precedent as recommended by Dudley and Moll (1969) and Hallauer and Miranda (1988). While variance component estimates for fruit number and fruit weight varied greatly across locations, estimates for primary branch number and average weight per fruit remained comparatively constant. The magnitude of the variance component estimates for fruit number and

Table 4 Percentage of progeny located on the extremes of parental and mid-parent values of melon (*Cucumis melo* L.) yield-formation factors analyzed for 119 F_3 families derived from a cross between USDA 846-1 (P_1), 'Topmark' (P_2)based on plants grown at Arlington and Hancock, Wisconsin in 2001

Arlington	Percentage of progeny values					
	USDA 846-1 (P_1)		'Topmark'(P_2)		Mid-parent[c]	
Trait	Above[a]	Below[b]	Above	Below	Above	Below
Days to anthesis	5	–[d]	–	17	42	58
Percentage of plants with early pistillate flowering/plot	9	–	–	10	38	62
Primary branch number	0	–	–	0	45	55
Fruit number/plant	–	8	29	–	66	34
Fruit weight/plant (kg)		3	58		82	18
Average weight/fruit (kg)	58	–	–	18	68	32
Percentage of plants predominantly crown fruit set/plot	0	–	–	0	3	97
Percentage of plants with early maturing fruit/plot	0	–	–	0	17	83
Hancock						
Primary branch number	0	–	–	0	32	68
Fruit number/plant	5	–	–	15	21	79
Fruit weight/plant (kg)	1	–	–	3	29	71
Average weight/fruit (kg)	–	29	43		59	41
Percentage of plants predominantly crown fruit set/plot	12	–	–	0	56	44
Percentage of plants with early maturing fruit/plot	9	–	–	45	31	69

[a] Families above the parental mean

[b] Families below the parental mean

[c] Families above or below the mid-parental value

[d] Only percentages above the larger parental value and below the smaller parental value are presented

Table 5 Phenotypic correlations among yield-related traits in 119 F_3 melon (*Cucumis melo* L.) families derived from a cross between USDA 846-1 (P_1) and 'Topmark' (P_2) evaluated at Arlington (upper diagonal) and Hancock (lower diagonal), Wisconsin in 2001

Trait	Days to anthesis (DA)	Percentage of plants with early pistillate flowering/plot (PPF)	Primary branch number(PB)	Fruit number per plant(FN)	Fruit weight/ plant (kg; FW)	Average weight/ fruit (kg; AWF)	Percentage of plants with predominantly crown fruit set/ plot (PCF)	Percentage of plants with early maturing fruit/plot (PMF)
DA	–	−0.58***[a]	−0.07 n.s.	0.13 n.s.	−0.07 n.s.	−0.17*	−0.10 n.s.	−0.24**
PPF		–	−0.02 n.s.	−0.21*	0.04 n.s.	0.24**	0.17*	0.24**
PB			–	0.03 n.s.	0.05 n.s.	0.01	0.25**	0.14 n.s.
FN			0.23**	–	0.47***	−0.76***	−0.52***	−0.18*
FW			0.20***	.61***	–	0.16*	−0.3***	−0.21*
AWF			−0.21*	−0.7***	0.27***	–	0.41***	0.07 n.s.
PCF			−0.09 n.s.	−0.48***	−0.22*	0.32***	–	0.36***
PMF			−0.07 n.s.	−0.28***	−0.20*	0.12 n.s.	0.8***	–

[a] n.s.,*,**,***, and non-significant or significant at $P \leq 0.05$, 0.01, and 0.001

Table 6 Genetic and environmental components of variance, and heritabilities and their standard errors for yield-formation factors in 119 F_3 melon (*Cucumis melo* L.) families derived from a cross between USDA 846-1 (P_1) and 'Topmark' (P_2) tested at Arlington and Hancock, Wisconsin in 2001

Genetic parameter[a]	Primary branch number	Fruit number per plant	Fruit weight per plant (kg)	Average fruit weight (kg)
Arlington				
$\sigma^2_{\bar{F}3}$	0.18 ± 0.04	0.48 ± 0.09	0.89 ± 0.16	0.06 ± 0.01
σ^2_A	0.24 ± 0.09	0.47 ± 0.08	0.53 ± 0.12	0.00
σ^2_D	−0.21 ± 0.16	0.06 ± 0.14	1.46 ± 0.22	0.25 ± 0.02
σ^2_{PP}	0.69 ± 0.02	2.14 ± 0.05	3.64 ± 0.09	0.18 ± 0.01
σ^2_{PF}	0.26 ± 0.04	0.66 ± 0.11	1.19 ± 0.19	0.07 ± 0.01
h^2_{NP}	0.17 ± 0.06	0.11 ± 0.02	0.07 ± 0.02	0.00
h^2_{NF}	0.91 ± 0.33	0.72 ± 0.12	0.45 ± 0.10	0.00
h^2_{BP}	0.17 ± 0.06	0.12 ± 0.05	0.27 ± 0.05	0.49 ± 0.04
h^2_{BF}	0.91 ± 0.33	0.75 ± 0.18	0.79 ± 0.15	0.87 ± 0.08
n	3.46	−0.86	−0.58	–[b]
Hancock				
$\sigma^2_{\bar{F}3}$	0.21 ± 0.04	0.04 ± 0.01	0.09 ± 0.02	0.05 ± 0.01
σ^2_A	0.24 ± 0.10	0.05 ± 0.02	0.04 ± 0.02	0.00
σ^2_D	−0.15 ± 0.19	−0.04 ± 0.04	0.20 ± 0.05	0.20 ± 0.02
σ^2_{PP}	0.89 ± 0.02	0.58 ± 0.02	0.74 ± 0.02	0.30 ± 0.01
σ^2_{PF}	0.29 ± 0.05	0.10 ± 0.02	0.15 ± 0.03	0.07 ± 0.01
h^2_{NP}	0.14 ± 0.06	0.04 ± 0.02	0.03 ± 0.02	0.00
h^2_{NF}	0.86 ± 0.35	0.51 ± 0.23	0.28 ± 0.16	0.00
h^2_{BP}	0.14 ± 0.06	0.04 ± 0.02	0.16 ± 0.05	0.34 ± 0.07
h^2_{BF}	0.86 ± 0.35	0.51 ± 0.23	0.64 ± 0.25	0.81 ± 0.42
n	2.28	−0.27	−1.35	–[b]
	Days to anthesis	Early pistillate flowering/plot	Predominantly crown fruit set/plot	Early maturing fruit/plot
h^2_{BF} (Arligton)	0.63 ± 0.11	0.64 ± 0.14	0.60 ± 0.14	0.62 ± 0.14
h^2_{BF} (Hancock)	–[c]	–	0.66 ± 0.14	0.63 ± 0.11

$\sigma^2_{\bar{F}3}$, σ^2_A, σ^2_D, σ^2_{PP}, σ^2_{PF}, h^2_{NP}, h^2_{NF}, h^2_{BP}, h^2_{BF}, and n are variation among F_3 family means, additive genetic variance, dominance genetic variance, phenotypic variance of individual plants within F_3 families, phenotypic variance of F_3 family means, narrow-sense heritability based on individual plants within F_3 families, narrow-sense heritability based on F_3 family means, broad-sense heritability based on individual plants within F_3 families, broad-sense heritability based on F_3 family means, and minimum number of effective factors, respectively

[b] Calculations not possible due to zero value of σ^2_A

[c] Data not available at Hancock Wisc

weight were higher at AR than at HCK. The additive genetic variance estimates for primary branch number and fruit number were positive at both AR and HCK, and the dominance variance estimates for these traits were negative or small in magnitude when compared to their additive variance estimates. In contrast, the magnitude of additive genetic variance for fruit weight and average weight per fruit at both locations was small when compared to their associated dominance variances.

Heritability estimates

Broad-sense heritabilities for days to anthesis (0.63; AR only), early pistillate flowering (0.64; AR only), predominantly crown fruit set [0.60 (AR) and 0.66 (HCK)], and early maturing fruit [0.62 (AR) and 0.72 (HCK)] (Table 6). Narrow-sense heritabilities were 0.91 (AR) and 0.86 (HCK) for primary branch number, 0.72 (AR) and 0.51 (HCK) for fruit number, 0.45 (AR) and 0.28 (HCK) for fruit weight,

and zero (AR) and 0.06 (HCK) for average weight per fruit.

Minimum number of effective factors

Estimates of the minimum number of effective factors (n) for yield for primary branch number were higher at AR ($\sim$4) than at HCK ($\sim$2) (Table 6). Estimates of (n) were consistently negative for all other traits examined, regardless of the location.

Discussion

The inheritances of the yield-formation traits examined are complex, and predictably the expression of these traits is dramatically affected by growing environment (e.g., soil type and climatic conditions). Some of these traits are directly related to yield (fruit number and weight) and others are associated with harvest timing (days to anthesis) and plant habit related to source/sink relationships (primary branch number); all of which influence crop management. The differences detected between parental lines and among F_3 families for many of the traits examined (Tables 3 and 4) requires a consideration of genotypic and environmental factors that may influence response to selection (Tables 1 and 2). Plant competition (i.e., within row spacing) is a major factor that can affect melon productivity (Bhella 1985; Davis and Meinert 1965; Knavel 1988; Maynard and Scott 1998; Mendlinger 1994; Zahara 1972). The plant spacing used in the present study (7,143 plants/ha), allowed for optimum plant development under Wisconsin conditions for the architectural types examined (Kultur et al. 2001). Thus, the differences observed among the genotypes examined herein are likely unrelated to environmental effects due to plant competition (for nutrients and space).

Most of the genotypes examined herein generally produced higher fruit number and weight per plant at AR than at HCK. However, the size of each fruit (average fruit weight) was small at AR when compared to that at HCK, and the percentage of plants with predominantly crown fruit set per plot and the percentage of plants with early maturing fruit per plot were lower at AR than HCK (Table 3). Given the percentage contribution of locations (L = high %) and the locations x family (L × F = low %) to the total variance and the high Spearman (rank) correlations coefficients ($r_s \geq 0.5$) between locations (Tables 1 and 2), fruit number and average weight per fruit were mostly affected by G × E interactions due to trait magnitude changes. In contrast, fruit weight, predominantly crown fruit set, and early maturing fruit were mainly affected by G × E interactions due to changes in the direction of the response (L = low %, L × F = high %, and $r_s \leq 0.5$). The comparatively heavy soil at Arlington contains higher organic matter (3.1% OM), nutrient content, and water-holding capacity than the sandy soil at Hancock (0.6% OM) (Kultur et al. 2001). Such differences in soil conditions produced plants that grew more rapidly ($\sim$2×'s) and larger ($\sim$1 m vs. $\sim$3 m in diameter) at AR than at HCK (by visual inspection). Thus, it is likely that soil differences between locations contributed dramatically to the observed variation in fruit development (Tables 3 and 4). Source-sink relation differences among genotypes (e.g., fractal vs. vining) likely also contributed to the variation in the genotypic performance (i.e., changes in rank) across environments for fruit concentration, maturity characteristics, and total yield (Hughes et al. 1983; Kubicki 1962; Kultur et al. 2001; McGlasson and Pratt 1963). These results indicate that breeding for high yielding melon cultivars with early, basally concentrated yield will require multiple location testing of progeny derived from complex breeding strategies (e.g., advanced selfing and backcrossing).

Primary branch number in all generations remained comparatively constant across locations (Tables 1 and 3). Spearman (rank) correlations between environments indicated that the interactions between family and environment were mostly due to changes in magnitude and not in the direction of the response in different environments (Table 1). These data are also consistent with those of Kultur et al. (2001) in melon, and Serquen et al. (1997) and Fazio (2001) in cucumber (*Cucumis sativus* L.) who reported that environmental effects (e.g., growing location and planting density) and G × E interactions are comparatively unimportant in determining branching patterns in diverse plant types.

The use of highly branched, dwarf melon types (birdnest types) has been proposed to increase melon yield (Nerson et al. 1983; Nerson and Paris 1987;

Paris et al. 1982, 1984, 1985). Modification of source-sink relations to increase yield may be accomplished by increasing the number of fruit-bearing branches using genes resident in extreme fractal melon germplasm. Given the consistency of primary branch number production over distinct environments, highly branched fractal genotypes are recoverable in early generations (e.g., F_2 population; Staub et al. 2004; Zalapa et al. 2004). If enough variability can be preserved, simple recurrent selection could be employed using these selections to increase desirable alleles for flowering, and fruiting characteristics prior to inbred line extraction (Staub et al. 2004; Zalapa et al. 2004). Moreover, the possibility of marker-assisted selection (MAS) for increasing yield during population development and/or inbred line extraction using highly branched germplasm is supported by the fact that several environmentally independent QTL for primary branch number were localized in close proximity with QTL for fruit number and weight per plant in a recombinant inbred line population derived from these F_3 families (Zalapa 2005; Zalapa et al. 2007).

Trait correlations are important when introgressing genes from exotic sources that alter plant architecture. The correlations between yield-formation factors reported herein (Table 5) are consistent with correlations reported in diverse melon genotypes (Abdalla and Aboul-Nasr 2002; Kultur et al. 2001; Lippert and Hall 1982; Taha et al. 2003). Low to moderately high desirable and undesirable correlations between yield-formation factors were observed in this "fractal" melon population. The positive correlations between primary branch number with fruit number, fruit weight, and predominantly crown fruit set, suggests that selection for higher number of primary branches in this population will likely produce plants with relatively high early, basally concentrated yield. However, such correlations were low ($r = \sim 20$), and the negative correlation between primary branch number and average weight per fruit indicates that selection for primary branch number will result in plants that produce relatively small fruits. Likewise, although selection for increased fruit number per plant will likely increase total fruit weight per plant, the size of each fruit and the number of basally concentrated fruit might be expected to decrease while the fruit maturation period in the selected genotypes may increase. Correlation analyses also suggest that selection for earlier flowering date will result in earlier pistillate flowering, and in turn in early yield. Similarly, selection for higher fruit weight per plant will decrease the number of basally concentrated fruit with a concomitant increase in fruit maturation period. Finally, selection for increased fruit size will likely increase the number of basally concentrated fruit and early yield. Thus, although exceptional phenotypes of potential economic importance were observed among the F_3 families examined (Table 4; percentage of transgressive segregant families), the proper alignment of unique alleles for earliness, high yield, crown yield concentration, and early fruit maturity will likely be complicated and will require index selection in backcross and selfed progeny (e.g., dominantly inherited traits). The ability to align such alleles in this population could be augmented by the marker-assisted genotyping to allow for selection of early, high yielding, monoecious plants.

The characterization of additive and dominance variation components in this population provides critical information useful for breeding (Kearsey and Pooni 1996). For instance, primary branch number and fruit number per plant exhibited mainly additive genetic variance, while fruit weight per plant and average weight per fruit demonstrated mainly dominance genetic variance (Table 6). In inbred populations, the additive variance is expected to be higher than the dominance variance, and thus in this population the importance of dominance variance for fruit weight per plant and average weight per fruit was evident and corroborated findings of Zalapa et al. (2006). The high-parent and/or mid-parent heterosis [i.e., transgressive segregants (%); Table 4] observed for fruit weight per plant and average weight per fruit likely indicates strong dominance effects (as combinations of parental alleles) for these traits which also corroborates Zalapa et al. (2006) who employed a classical six generation means analysis of the same parental mating.

Estimates of broad- and narrow-sense heritabilities based on F_3 family performance were larger than those based on individual F_3 plant performance. Thus, selection based on family performance would clearly be more effective than that based on individual plants for all traits. The increase of unique alleles controlling important traits such as branching and fruit number and strategic alignment with earliness

and other fruit yield, fruit concentration and maturity characteristics in this population could be accomplished by using a simple biparental recurrent selection scheme of extreme-fractal, high yielding germplasm identified herein (F_3 families 108, 113, 67, 30, 107, 30, 80, 18, 56, 83, 12, 54, and 59). Thereafter, family or pedigree selection with inbreeding might be performed (to convert dominance genetic variance to additive variance) for inbred line extraction using multiple evaluation environments and extensive replication to minimize environmental effects. Where traits are controlled mainly by dominant effects, such inbred lines could be used strategically to exploit heterotic effects (e.g., diallel analysis).

Estimates of effective factors (n) are usually biased downward, (sometimes even close to zero or negative) due to dominance, epistasis, and G × E interactions (Kearsey and Pooni 1996). Thus, the values of (n) reported herein should be considered underestimates since dominance and/or epistatic effects were detected by Generation Means Analysis (Zalapa et al. 2006), and G × E interactions were detected for most traits, except for primary branch number examined. Calculations of (n) for primary branch number ranged from two to four, fruit number and weight values were negative, and estimates for average fruit weight were not possible due to the lack of additive variance. Estimates of the numbers of genes affecting yield-formation traits in melon can be further defined using QTL analysis (Austin and Lee 1996; Dijkhuizen and Staub 2003; Quijada et al. 2004; Septiningsih et al. 2003). In fact, multiple factor control of fruit number (9), fruit weight (12), and average fruit weight (5) and epistatic interactions were confirmed by QTL analysis using a recombinant inbred line population derived from the F_3 families used herein (Zalapa 2005; Zalapa et al. 2007).

Manipulation of plant architecture (e.g., primary branch number) may allow for the development of extreme fractal genotypes with early, uniform flowering and concentrated yield (Table 6). Variation within and among F_3 families for all traits examined indicates that the creation of advanced inbred generations would allow for more extensive genetic analyses. In fact, recombinant inbred lines (currently F_9) derived from these F_3 progeny differ in traits not examined in this study such as internode length and growth habit (e.g., reduced stature genotypes; Nerson et al. 1983; Nerson and Paris 1987; Paris et al. 1982, 1984, 1985) (data not presented; Zalapa 2005). Such traits likely have demonstrable affects on source/sink relationships, and consequently yield. In this regard, the broad- and narrow-sense heritability estimates indicate that, in the F_3 population studied herein, it may be possible to identify and select highly extreme-fractal genotypes with early, uniform flowering and concentrated fruit-setting ability. Such genotypes would be particularly amenable for once-over and/or machine harvesting operations since they would ideally set three to four fruit "simultaneously" (within a 1–2 day period of time) near the crown of the plant (i.e., concentrated setting). The development of these fractal melon genotypes will, however, require selection and testing at commercial plant densities (~14,285 plants/ha) to incorporate (fixation of alleles) high primary branch number while maintaining variability for earliness, fruiting, and maturity.

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